

Spatial and Temporal Variability in South San Francisco Bay (USA). II. Temporal Changes in Salinity, Suspended Sediments, and Phytoplankton Biomass and Productivity Over Tidal Time Scales

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Short-term variability of a conservative quantity (salinity) and two nonconservative quantities (chlorophyll *a*, suspended particulate matter) was measured across a sampling grid in the South San Francisco Bay estuary. Surface measurements were made every 2 h at each of 29 (or 38) sites, on four different dates representing a range of tidal current regimes over the neap-spring cycle. From the distribution of phytoplankton biomass (chlorophyll *a*) and turbidity (SPM), we also estimated daily productivity and its variability at each site over the four tide cycles. As a general rule, both chlorophyll *a* and SPM concentrations varied about 50% from their tidal-means. However derived daily productivity varied less (about 15% from the mean) over a tidal cycle. Both chlorophyll *a* and SPM varied periodically with tidal stage (increasing on ebbing currents), suggesting that the short-term variability results simply from the tidal advection of spatial gradients. Calculation of the advective flux (current speed times spatial gradient) was used to test this hypothesis. For surface salinity, most (70–80%) of the observed intratidal variability was correlated with the tidal flux, both in the deep channel and over the lateral shoals. However the short-term variability of SPM concentration was only weakly correlated with the advective flux, indicating that local sources of SPM (resuspension) are important. Hourly changes in chlorophyll *a* were highly correlated with the advective flux in the deep channel (implying that phytoplankton biomass is conservative over short time scales there); however, chlorophyll *a* variability was only weakly correlated with the advective flux over the shoals, implying that local sources/sinks are important there. Hence, the magnitude and mechanisms of intratidal variability differ among constituents and among bathymetric regimes in this estuary.

Introduction

Much of phytoplankton ecology addresses questions of variability, such as changes in biomass, community composition, or primary productivity across a spectrum of temporal

and spatial scales. Historically, emphasis has been placed on temporal variability at the longer time scales (weekly, seasonal). However short-term (e.g. hourly) variability can also be substantial, and in some cases of equal magnitude to that occurring at the longer time scales (Harris, 1980). Short-term variability of phytoplankton biomass can be driven by either high frequency physical forcings or biological processes. Examples of the former include vertical displacements of chlorophyll gradients by internal waves (e.g. Therriault & LaCroix, 1976; Sarabun *et al.*, 1986), resuspension of benthic microalgae by wind waves (Demers *et al.*, 1987), and redistributions of phytoplankton biomass by wind-driven surface currents (Harris & Trimbee, 1986) or river-driven currents (Litaker *et al.*, 1987). Examples of the latter include diel vertical migrations of dinoflagellates (Haas *et al.*, 1981), diel periodicity of zooplankton grazing (inferred, e.g. by Whitley & Wirick, 1983), high frequency periodicity of chlorophyll *a* synthesis (Auclair *et al.*, 1982), and synchronous cell division.

Many of these mechanisms of short-term variability can exist in all water bodies, including lakes and the open ocean. In estuaries and shallow coastal waters an additional source of short-term variability is the tides, which can alter phytoplankton biomass through, for example, resuspension of benthic microalgae (Roman & Tenore, 1978) or horizontal advection. The partitioning of phytoplankton temporal variability among these mechanisms is difficult, and no consistent generalizations have emerged concerning the magnitude of short-term variability or the primary source(s) of that variability in estuaries. Such information is required before we can: (1) resolve phytoplankton variability at longer time scales (e.g. distinguish the seasonal variations in biomass from intratidal variability); (2) understand the mechanisms through which physical processes influence phytoplankton populations; or (3) design efficient schemes for sampling plankton in tidal estuaries.

A primary objective of the study described here was to quantify short-term variability of phytoplankton biomass in a mesotidal estuary (South San Francisco Bay), and to estimate that component of variability associated with tidal advection. A second, parallel objective was to characterize short-term variability in the distribution of primary productivity resulting from changes in the distribution of biomass. Such estimates can be meaningful in temperate estuaries where nutrient availability is high and phytoplankton productivity is largely a function of biomass, measured as chlorophyll *a*, and light availability measured as photic depth (e.g. Cole & Cloern, 1987). Results presented here complement the preceding paper (Powell *et al.*, 1989), which characterizes mesoscale spatial variability in this estuary.

Methods

South San Francisco Bay is a brackish embayment having two distinct bathymetric regimes—a narrow, longitudinal channel (10–15 m deep) flanked by a broad expanse of subtidal shoals to the east (Figure 1). Previous studies have demonstrated that physical properties (e.g. current speed—Cheng & Gartner, 1985) and chemical/biological properties (nutrient concentrations, phytoplankton biomass, turbidity—Cloern *et al.*, 1985) can vary significantly across this bathymetric gradient. Hence a major consideration in the design of this field experiment was to contrast short-term variability along the channel with that observed over the eastern shallows.

The experimental design involved repeated measurements at a grid of fixed locations (Figure 1), over a 12-h period (0600 h–1800 h PST) on four dates in 1987. These dates

chlorophyll *a* were constant within and among dates, so all pairs of *in vivo* fluorescence and extracted chlorophyll *a* were pooled into one highly significant linear regression (see Figure 3 of the preceding paper). We therefore used calculated chlorophyll *a* as a measure of phytoplankton biomass in this study.

From the measured chlorophyll *a* and SPM concentration at each site, we also estimated a potential daily primary productivity P' , from the empirical function of Cole and Cloern (1987):

$$P' = 150 + 0.73 [BZ_p I_o]. \quad (1)$$

Here P' is productivity in the photic zone ($\text{mg C m}^{-2} \text{d}^{-1}$), B is chlorophyll *a* concentration, Z_p is photic depth estimated from SPM concentration, and I_o is irradiance ($\text{Einst. m}^{-2} \text{d}^{-1}$). Powell *et al.* (1989) present more detail of these methods. These data were then used to produce maps of near-surface salinity, chlorophyll *a*, SPM, and productivity distribution for six different phases of the tidal cycle each date (note that stations below the San Mateo Bridge were not sampled on 26 February or 9 March, and only five sampling circuits were completed on 7 April).

For each sampling period, tidal heights were predicted on the basis of historical tide gauge records from the San Mateo Bridge (Cheng & Gartner, 1984). Currents were measured with Endeco-174 current meters at one shallow and one deep site located within the sampling grid (Figure 1). These current meters, placed near mid-depth at the shallow site and near-surface at the deep site, record time-averaged speed and instantaneous direction every 2 min. From these records we computed a time series of vector-averaged tidal currents at 30 min intervals during the field measurement periods.

Results

This study occurred during a period of low freshwater inflow; consequently, the water column was persistently well mixed (see Figure 7, Powell *et al.*, 1989). Salinity varied over a small range (about 25–28) on all four dates, and vertical salinity differences were always < 1.0 . Moreover, periodic collections of near-bottom water samples indicated that chlorophyll *a* was typically uniform with depth in the channel. The magnitude of the 1987 spring bloom (maximum chlorophyll *a* $< 10\text{--}15 \text{ mg m}^{-3}$) was small compared to years of high freshwater inflow (maximum chlorophyll *a* $> 50 \text{ mg m}^{-3}$), consistent with the hypothesis that bloom magnitude is directly related to the intensity and duration of river-driven density stratification (Cloern, 1984).

On all four dates the horizontal distributions of chlorophyll and near-surface SPM were highly dynamic over the tidal time scale. For example, Figure 2 shows the distributions of chlorophyll and SPM for the five different tidal phases sampled on 7 April. Sampling began near high water (\approx slack before ebb), when chlorophyll *a* concentration ranged from about 3 mg m^{-3} at the northern (seaward) stations to about $7\text{--}8 \text{ mg m}^{-3}$ at the southern (landward) stations. As the ebb current progressed, chlorophyll *a* concentration continuously increased at all sites and by the final sampling, near low water, chlorophyll *a* concentration ranged from $4\text{--}13 \text{ mg m}^{-3}$. These sequential maps show a progressive displacement of chlorophyll isopleths that roughly parallel the tidal streamlines. Note, for example, that between 1100 h and 1500 h (Figure 2) the 6 mg m^{-3} isopleth was displaced seaward, and further in the channel (where currents are strongest) than in the eastern shallows. Note also the appearance of high chlorophyll water masses over the SE shallows near low tide. These patterns were reversed for flooding tides (e.g. 27 March), when

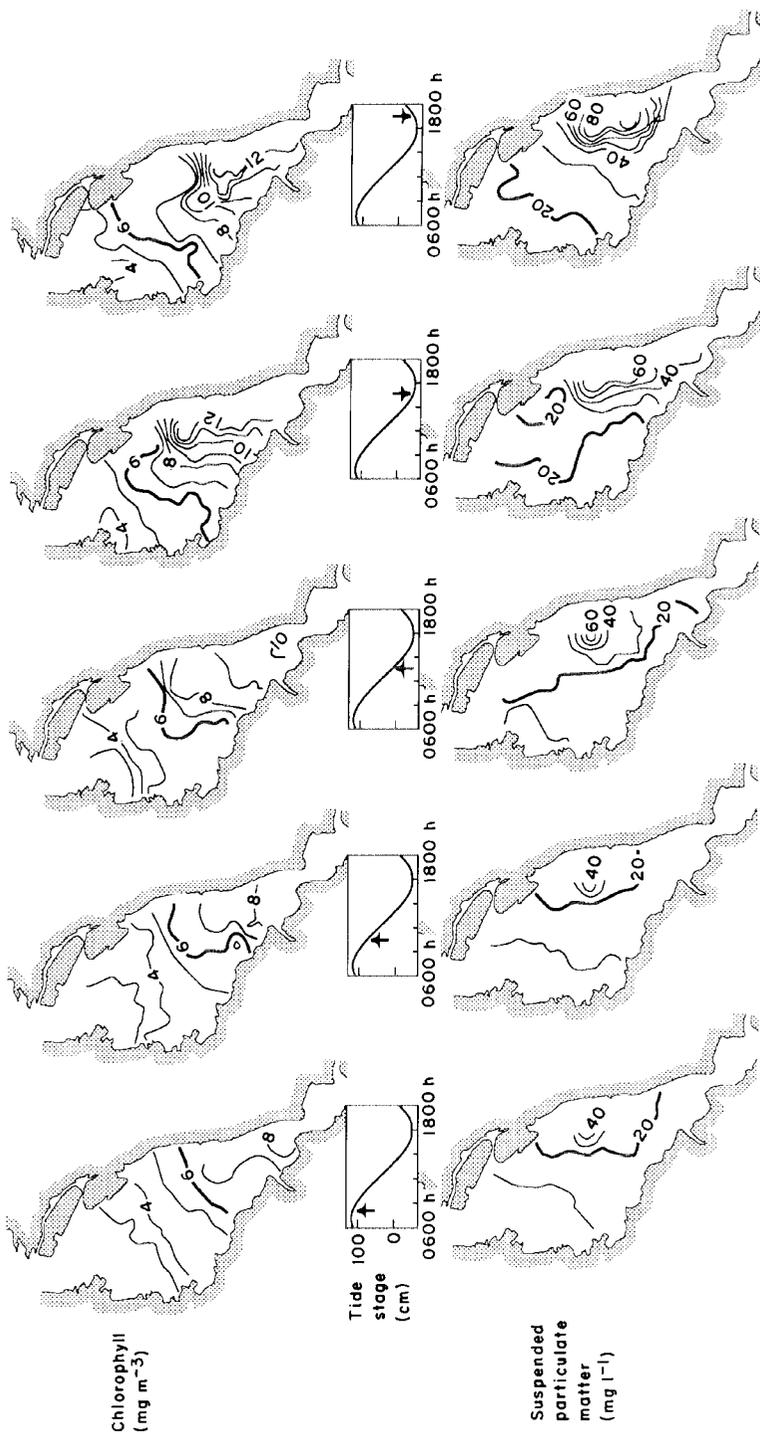


Figure 2. Surface contour maps of chlorophyll *a* and SPM concentrations for the five tide phases sampled on 7 April 1987.

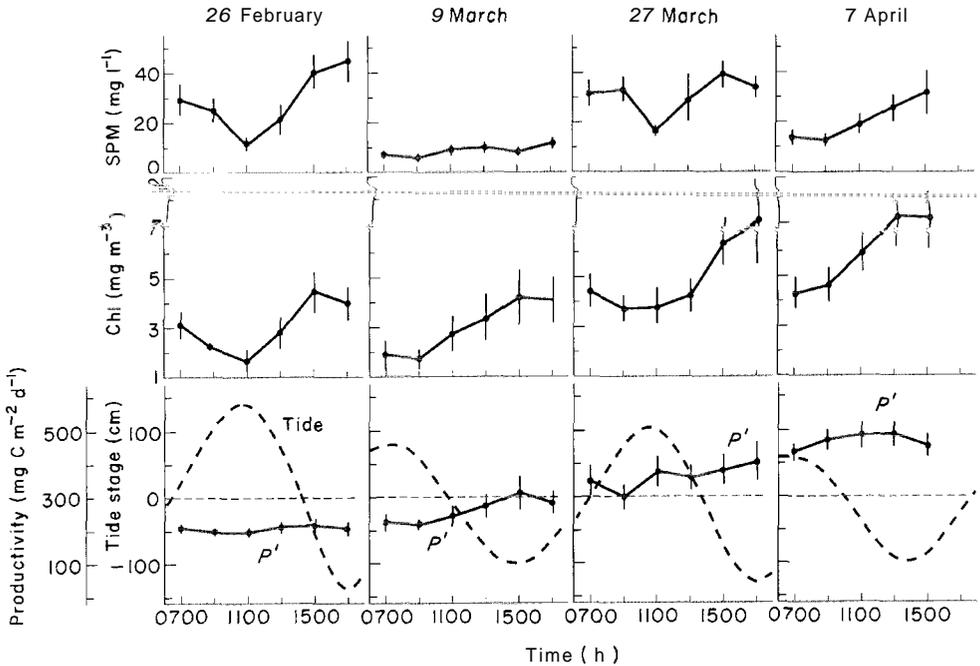


Figure 3. Time series of measured SPM and chlorophyll *a* concentrations, derived productivity P' , and predicted stage for the four sampling dates in 1987 (the tides of this subestuary approximate standing waves, so tidal currents and stage are nearly in phase---Cheng & Gartner, 1985). Each point represents the mean of measurements made at all (29 or 38) sites within a 2-h sampling period. Vertical bars show 95% confidence intervals around these means, indicating spatial variability within the sample grid.

chlorophyll isopleths were displaced landward along the channel and to the SE over the eastern shallows, and when decreasing chlorophyll levels were observed over the shoals.

Distributions of SPM were similarly dynamic over the tidal cycle. On 7 April (Figure 2), SPM concentrations ranged from 5–30 mg l^{-1} around high tide and progressively increased to 10–80 mg l^{-1} at the end of sampling near low tide. Note the large displacement of SPM isopleths (e.g. the 20 mg l^{-1} -isopleth) in the channel, and the appearance of high turbidity over the SE shallows at low water. On this date, winds were calm in the morning and accelerated to 7 m s^{-1} (from the NW) in the afternoon when the highest SPM concentrations were observed.

In order to represent these short-term dynamics in a simple manner, we calculated spatial means of SPM, chlorophyll *a*, and P' for each sampling circuit, and then plotted daily time series of these means along with predicted tidal heights (Figure 3). Error bars are 95% confidence limits around these means, and represent spatial variability over the sampling grid (29 sites on 26 February and 9 March; 38 sites on 27 March and 7 April). On all four dates, there were statistically significant differences in mean SPM concentration between high and low water. The magnitude of intratidal variability was about 2–5 fold for mean SPM; it was smallest on the neap tide of 9 March and greatest on the spring tide of 26 February. Note further that the variations in mean SPM appeared to be periodic and generally mirrored tidal height such that SPM concentration was often highest on low tide. An obvious exception to this periodic variability was the neap tide on 9 March when mean SPM concentration was small throughout the tidal cycle (Figure 3).

TABLE 1. Mean values of chlorophyll a, SPM, and derived productivity P' for each sampling date in 1987. Mean values were calculated from individual measurements at n sampling sites over m phases of the tide (sampling circuits). Also shown for each quantity is the coefficient of tidal variation ($CV = \text{mean, for } n \text{ sampling sites, of } [100SD_i/\bar{x}_i]$, where $SD_i = \text{standard deviation among sampling circuits at site } i$, and $\bar{x}_i = \text{tidally-averaged mean at site } i$)

Cruise date	A 26 Feb	B 9 March	C 27 March	D 7 April
Number of sampling stations	29	29	38	38
Number of sampling circuits	6	6	6	5
Mean chlorophyll (mg m ⁻³)	3.1	3.0	5.0	5.9
CV	47%	44%	34%	28%
Mean SPM (mg l ⁻¹)	28.6	9.3	31.3	25.6
CV	54%	41%	38%	45%
Mean P' (mg C m ⁻² d ⁻¹)	210	260	360	470
CV	10%	18%	19%	12%

Variability of mean chlorophyll a concentration was similar to that for SPM. Significant intratidal differences occurred on all four dates and in each case mean chlorophyll concentration varied inversely with tidal height. These observations indicate significant short-term variability in phytoplankton biomass. However, the estimated rate of production P' exhibited much less variability (Figure 3). Only on one date (9 March) did the spatial mean of P' vary significantly over the tidal cycle.

To quantify intratidal variability at individual sites, we calculated the coefficients of variation for SPM, chlorophyll a, and P' for each site ($CV_i = 100 [SD_i/\bar{x}_i]$, where $SD_i = \text{standard deviation}$ and $\bar{x}_i = \text{tidal-cycle mean at site } i$). These values were then averaged over all sites to give an index of mean intratidal variability ($CV = [\sum CV_i]/n$; $n = \text{number of sample sites}$), which ranged from 28–47% for chlorophyll a and 38–54% for SPM concentration (Table 1). Hence the intratidal variability of SPM and chlorophyll a concentration at an individual site was about 40–50% of the tidally-averaged mean. However, this coefficient of intratidal variability was only 10–19% for estimated daily productivity P' (Table 1).

Discussion

Magnitude of intratidal variability

These field measurements demonstrate that the short-term variability of both chlorophyll and SPM concentration is statistically significant in South San Francisco Bay. Moreover, the qualitative nature and magnitude of intratidal variability are similar for these two constituents. This is unexpected because the mechanisms of variability are potentially very different for phytoplankton biomass and suspended sediment concentration. The stability of estimated productivity was also unexpected, and this results from the short-term covariability of SPM and chlorophyll a (Figure 3). On all four sampling dates, the spatial mean of chlorophyll a was highly correlated with the spatial mean of SPM over the tidal cycle (r ranged from 0.62–0.95). P' is proportional to chlorophyll/SPM (equation 1), so when chlorophyll and SPM covary, incremental increases in productivity resulting

from increases in biomass are offset by corresponding increases in SPM that reduce the photic depth.

Note that P' is not an estimator of instantaneous productivity because it ignores diel periodicities of photosynthesis. Rather, P' is an estimator of daily productivity inferred from instantaneous measures of biomass and light availability. However, variability of P' does estimate the variability expected from sequential 24-h incubations at a given site, beginning at different phases of the tidal cycle. Results presented here suggest that the magnitude of this variability is small relative to variations in biomass. Hence, in this estuary, field programs designed to map productivity are less susceptible to errors associated with intratidal variability than are parallel programs to map biomass.

Results of these experiments define the magnitude of short-term variability, and hence the limits of our ability to detect changes in phytoplankton biomass or productivity at longer time scales. The spatial mean of chlorophyll concentration varied up to a factor of 3 (maximum $\overline{\text{Chl}}$:minimum $\overline{\text{Chl}} \leq 3$) over the tide cycle, so weekly or seasonal changes in biomass of this magnitude cannot be resolved from the intratidal variability. Similarly, mean SPM concentration varied somewhat less than a factor of 4, and mean P' varied less than a factor of 2 over the tidal time scale. These measures of variability are small relative to those previously observed at longer time scales. For example, near-weekly surface sampling in the South Bay channel demonstrated a 40-fold range of chlorophyll *a* concentration during 1983 (Cloern *et al.*, 1985). Most of this variability occurs during the spring bloom(s), when chlorophyll concentration can increase 10–20-fold over a period of weeks (Cloern, 1984). Results of this study indicate that such events represent real increases in phytoplankton biomass, and they can not be attributed to intratidal sampling error. Similar studies showed that over an annual cycle, SPM concentration can vary 50-fold (Wienke & Cloern, 1987) and daily primary productivity varies over 20-fold (Cole & Cloern, 1984). As a general rule, it appears that seasonal variability of phytoplankton biomass and productivity can be about an order of magnitude greater than the short-term variability observed here.

Intratidal variability of phytoplankton biomass has been examined in other tidal estuaries, and the sampling approach has commonly been to collect time series of measurements at one or several fixed locations (e.g. the Ecovariate program in the St Lawrence estuary—Demers *et al.*, 1979; multiple time series in Bahia San Quintin—Lara-Lara *et al.*, 1980; Millan-Nuñez *et al.*, 1982), or more rarely along a transect (e.g. Duedall *et al.*, 1977). These studies demonstrated a range of short-term variability similar to that observed in South San Francisco Bay; near-surface chlorophyll *a* concentration varies by about a factor of 2–5 in the St Lawrence estuary (Therriault & LaCroix, 1976), Bedford Basin (Lewis & Platt, 1982), apex of the New York Bight (Duedall *et al.*, 1977), and the Newport River estuary (Stearns *et al.*, 1987). Moreover, similarities exist in the qualitative nature of this variability such that near-surface chlorophyll *a* concentration often varies inversely with tidal height, as observed here (e.g. Duedall *et al.*, 1977; Riaux & Douville, 1980; Riaux, 1981; Lewis & Platt, 1982).

Short-term variability of SPM concentration can be extreme in other estuaries. For example, Pejrup (1986) observed 20-fold variation of SPM concentration in the Danish Wadden Sea and attributed much of this variability to changes in wind speed and direction. Schubel (1971) observed a similar intratidal variability of near-bed SPM concentration in the upper Chesapeake Bay, and this variability was correlated with current speed. In the mesotidal Tagus Estuary, Vale and Sundby (1987) observed nearly 40-fold variation of SPM concentration over one (spring) tide cycle, and they attributed this

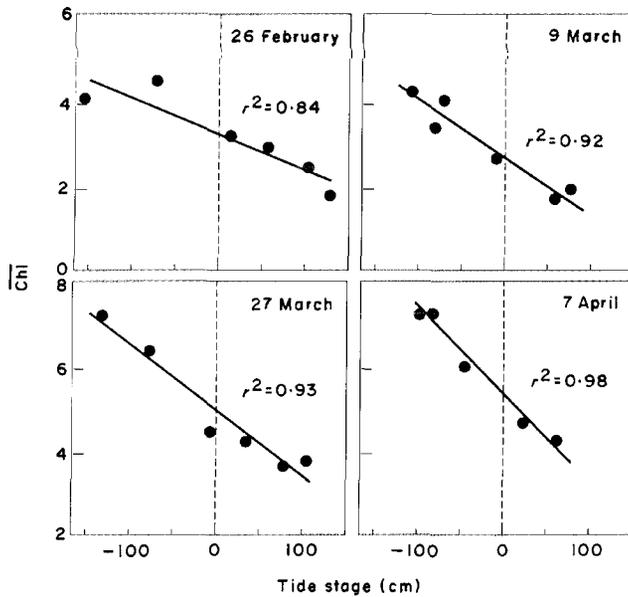


Figure 4. Correlations between spatially-averaged chlorophyll *a* concentration and predicted tide stage for the four sampling dates.

semidiurnal variability to tidal erosion and advection of suspended sediments off of mud-flats. Over the tidal time scale, then, SPM concentration can be much more dynamic than phytoplankton biomass in estuaries.

Although diel variability of algal photosynthesis has been studied extensively (e.g. Harding *et al.*, 1982; Legendre *et al.*, 1985), short-term variability in the measurement of *daily* primary productivity has not been addressed previously in estuaries. Our results indicate that this component of variability is small compared to biomass variability in South San Francisco Bay. However this generality may not hold in other estuaries where chlorophyll and SPM concentrations are uncorrelated over the tidal time scale.

Mechanisms of Intratidal Variability

As explained previously, numerous mechanisms can generate short-term variability of phytoplankton biomass in estuaries, including tide- and wind-driven resuspension, diel growth, synthesis and grazing cycles, and vertical migrations. However, the periodic nature of chlorophyll variability (Figure 3) suggests that here, an important mechanism might simply be the redistribution of phytoplankton biomass by tidal currents. On all four dates, most (> 80%) of this variability in mean chlorophyll concentration was correlated with tidal stage (Figure 4), and thus tidal currents. If the horizontal gradients of chlorophyll are uniform along the tidal streamlines, this correlation indicates that tidal advection may be the dominant mechanism of short-term variability in South San Francisco Bay.

Comparable strong relations between SPM concentration and tidal stage were observed on two dates (26 February, 7 April), but the correlations were weaker on 9 March and 27 March (Figure 5). The weak correlation for 9 March reflects the uniform distribution (i.e. small spatial gradients) of SPM concentration on that date. Decreases in the mean SPM concentration between 26 February and 9 March (Figure 5) probably resulted from neap-spring differences in current speed and tidally-driven resuspension. On both dates

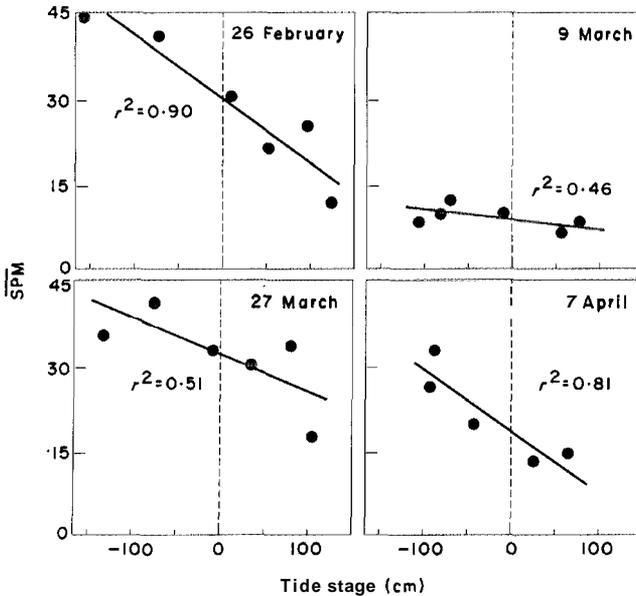


Figure 5. Correlations between spatially-averaged SPM concentration and predicted tide stage for the four sampling dates.

winds were calm, but maximum current speed in the channel decreased from 0.93 m s^{-1} on 26 February (a spring tide) to 0.64 m s^{-1} on 9 March (neap tide). Similar neap-spring variations in SPM concentration have been observed in other estuaries (e.g. Milliman *et al.*, 1984; Vale & Sundby, 1987). The weak correlation between SPM concentration and tide stage on 27 March (Figure 5) reflects another mechanism of SPM variability—riverine sources of suspended sediment. During the first half of March, discharge of the Sacramento-San Joaquin Rivers increased from <200 to $>1000 \text{ m}^3 \text{ s}^{-1}$ (Figure 4, Powell *et al.*, 1989). This event radically altered the distribution of SPM such that the horizontal gradients were nonuniform and nonlinear. Hence in this case a poor correlation between mean SPM concentration and tidal stage (Figure 5) might be expected.

The relations shown in Figures 4 and 5 suggest that tidal advection may be the predominant mechanism of short-term variability for phytoplankton biomass, that tidal advection may also be a predominant mechanism of short-term SPM variability under some conditions, but that other mechanisms (e.g. river sources, resuspension) may contribute to SPM variability observed at the tidal time scale. To explore these ideas, we estimated the local advective fluxes of chlorophyll and SPM at two sites, representing the deep channel (strong tidal currents) and eastern shallows (weaker currents), then compared these advective fluxes to the local concentration changes observed over the four tide cycles.

Specifically, in this vertically mixed estuary, if the net rate of concentration change for constituent C at position (x, y) is caused entirely by advection, then:

$$\partial C(x, y) / \partial t = -\mathbf{V} \cdot \nabla C \quad (2)$$

Note that measured values of $\partial C / \partial t$ will include the contributions from all sources and sinks (e.g. *in situ* production, grazing, resuspension, etc.). The measured advective term,

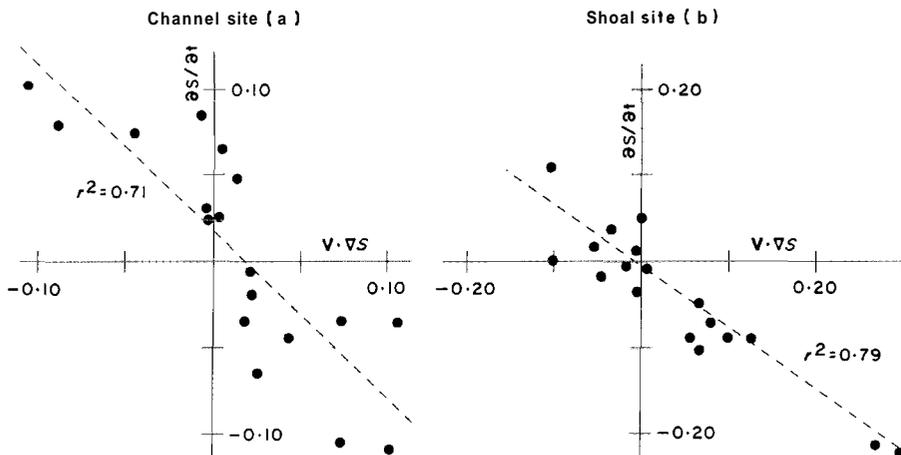


Figure 6. Observed short-term salinity changes $\partial S/\partial t$ (h^{-1}) vs. calculated advective fluxes $\mathbf{V} \cdot \nabla S$ (h^{-1}) around the two current meter locations in South San Francisco Bay (see Figure 1). Data points represent measurements from sequential 2-h sampling intervals on four dates.

$\mathbf{V} \cdot \nabla C$, where \mathbf{V} is the velocity vector, includes transport due to wind and residual circulations as well as tidal currents. Only when advection is the sole contributor will equation 2 hold.

As previously described, concentrations were measured on six occasions through each day. The mean spatial gradient (∇C), parallel to the principal current direction, and in the vicinity of the current meter locations, was calculated for each 2-h sampling period. A finite difference method was used incorporating measured concentrations at 9 stations at the channel site, and 4 stations on the shoal (see Figure 1). The average spatial gradient from successive sampling periods $[(\nabla C_j + \nabla C_{j+1})/2]$ was then multiplied by the average current velocity (which is closely parallel to the principal current axis) for the same period, giving $\mathbf{V} \cdot \nabla C$. The net time rate of change ($\partial C/\partial t$) was also estimated by finite difference as $[(\bar{C}_{j+1} - \bar{C}_j)/\Delta t]$ where \bar{C} is the mean concentration over the chosen stations.

The precision of this analytical technique was checked by comparing the advective fluxes and short-term variability of salinity (S), a conservative constituent. These results demonstrate that most ($> 70\%$) of the intratidal variability of salinity ($\partial S/\partial t$) was correlated with the estimated advective flux ($\mathbf{V} \cdot \nabla S$), at both the channel and shoal sites (Figure 6). For a conservative constituent, the short-term variability should be driven predominately by tidal advection and we expect close agreement between the observed net rate of change ($\partial S/\partial t$) and the estimated tidal flux ($\mathbf{V} \cdot \nabla S$). Hence we interpret the goodness of fits in Figure 6 as limits on the precision of this technique, which is subject to several errors (measurement errors, assumption of isotropic and linear spatial gradients, errors associated with finite difference approximations).

Similar analysis was done to characterize the short-term chlorophyll variability, and these results differed for the two sites. At the channel location there was very good agreement ($r^2 = 0.73$) between observed local changes in concentration and those predicted from tidal fluxes (Figure 7a). Hence in the deep parts of the estuary, where tidal currents are rapid and confined by sharp bathymetric transitions, the intratidal variability of chlorophyll is primarily due to the tidal advection of spatial biomass gradients (mean

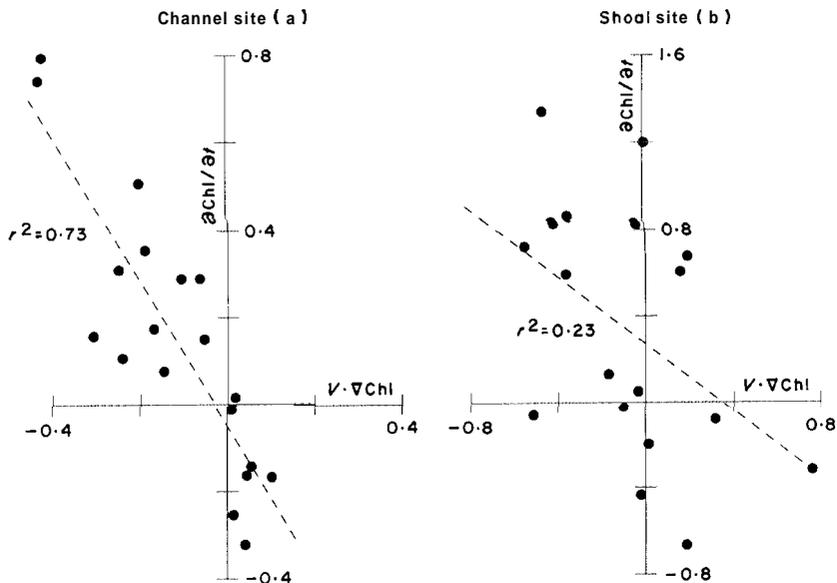


Figure 7. Observed short-term chlorophyll changes $\partial \text{Chl} / \partial t$ ($\text{mg m}^{-3} \text{h}^{-1}$) vs. calculated advective fluxes $V \cdot \nabla \text{Chl}$ ($\text{mg m}^{-3} \text{h}^{-1}$) around the two current meter locations in South San Francisco Bay (see Fig. 1).

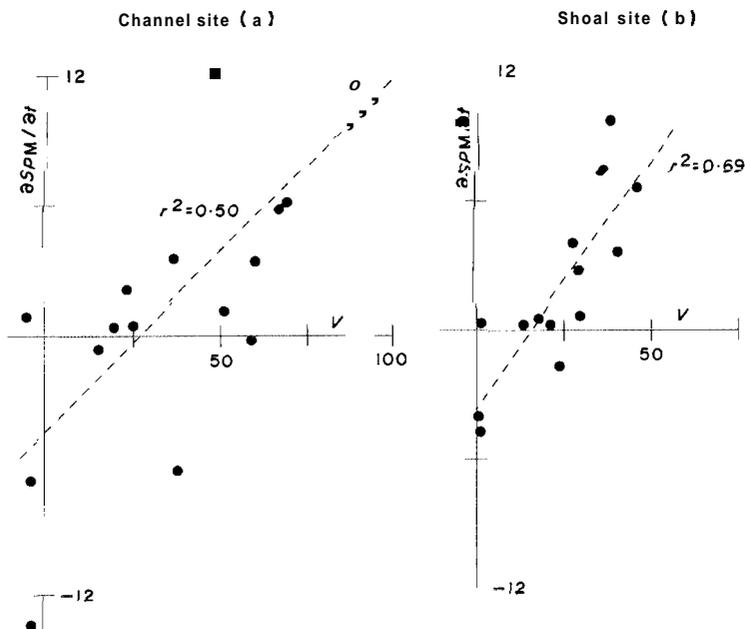


Figure 8. Observed short-term changes in SPM concentration $\partial \text{SPM} / \partial t$ ($\text{mg l}^{-1} \text{h}^{-1}$) vs. mean current speed (cm s^{-1}) around the two current meter locations in South San Francisco Bay. $\partial \text{SPM} / \partial t$ was calculated from sequential 2-h measurements; current speeds were averaged over the same 2-h periods. Plots include only those measurements made around ebbing or slack currents on the four sampling dates.

chlorophyll concentration was not correlated with time of day, so the short-term variability is not a result of diurnal biomass synthesis). The results of this analysis were equivocal for the shoal site, where there was only a weak correlation between $\partial\text{Chl}/\partial t$ and $\mathbf{V} \cdot \nabla \text{Chl}$ (Figure 7b). This weak correlation results from either (1) local sources or sinks for phytoplankton biomass with characteristic time scales comparable to the tidal fluxes, or (2) errors in the analysis, and, particularly, errors associated with approximating local gradients of chlorophyll from sparse data. Given the coarse spatial resolution of this sampling program, the second possibility may explain the poor agreement shown in Figure 7b. However, it is also likely that phytoplankton biomass may be more dynamic over the shallows than in the deep channel. For example, mean light availability and, hence, population turnover rate is higher over the shallows than in the deeper well-mixed channel (Alpine & Cloern, 1988). Additionally, the sediments of South San Francisco Bay contain high concentrations of chlorophyll a (Thompson et al., 1981), and the resuspension of benthic chlorophyll should be most evident over the shallows. Finally, the loss rate of biomass to benthic grazers, which may be the dominant phytoplankton sink in South Bay (Cloern, 1982), should scale inversely with water depth and therefore be most rapid over the shallows. Our results suggest that the mechanisms of short-term phytoplankton variability may vary spatially across bathymetric contours, reflecting differences in the relative importance of benthic-pelagic coupling. However, this hypothesis cannot be tested rigorously without finer scale sampling to reduce the magnitude of errors in calculating tidal fluxes.

Parallel analyses indicate that tidal advection may be only a small component of the short-term variability of SPM concentration. At the channel site there was no correlation between $\partial\text{SPM}/\partial t$ and $\mathbf{V} \cdot \nabla \text{SPM}$, and at the shallow site this correlation was weak ($r^2=0.38$). Again, these poor correlations may result from errors in the estimation of tidal SPM fluxes, but they may reflect other mechanisms of variability in the distribution of SPM. Whereas the spatial gradients of chlorophyll were relatively stable between dates, SPM distribution was much more dynamic and included gradient reversals following inputs of river-derived SPM (see Figure 10, Powell et al., 1989), and pronounced neap-spring differences in mean SPM concentration (Figure 3). Resuspension may also be an important mechanism of local change in SPM concentration, because $\partial\text{SPM}/\partial t$ was highly correlated with current speed, particularly on ebbing tides (Figure 8). Tidally-driven resuspension is presumed to be a primary mechanism of SPM variability in estuaries (e.g. Schubel, 1971; d'Anglejan, 1981; Vale & Sundby, 1987), and the strong correlations shown in Figure 8 indicate that this is true in South San Francisco Bay.

Temporal changes over the tidal time scales we have examined are not large—less than 50% in all cases. However, the magnitude of these changes can depend upon the size of the spatial gradients in the quantity under consideration. Equation 2 illustrates this effect. If ∇C is large, then $\mathbf{V} \cdot \nabla C$ will be large, and vice versa. For example, during the dry spring of 1987 the longitudinal gradients in chlorophyll a were smaller than those seen in wetter years (e.g. 1982). Had detailed measurements of temporal changes over a tidal cycle been taken in 1982, values substantially greater than 50% would have been observed. Processes other than direct river flow can potentially create large gradients, e.g. channel-shoal differences in *in situ* production of phytoplankton biomass or resuspension of particulate matter. Accordingly, one must be cautious when comparing temporal changes alone in the absence of information about spatial gradients (see the preceding paper).

An acute estimation problem can arise if substantial small-scale spatial variability exists in quantities such as chlorophyll a or SPM (Powell et al., 1986 have characterized

small-scale chlorophyll variability in South San Francisco Bay). Then expressions such as $\nabla \cdot \nabla C$ in equation 2 will be dominated by the large, rapidly varying ∇C term. Estimates of the gradient will be tedious to calculate, since they must incorporate much closely spaced, small-scale information. The large-scale estimates of the gradient from widely spaced points, as we have attempted here, will be severely flawed. This points to the need for some knowledge of 'sub-grid scale' behaviour at small spatial scales before estimates of temporal change can be made reliably.

In summary, we have observed short-term covariations of chlorophyll and SPM concentration that lead to stability in the horizontal distribution of daily productivity. Moreover, intratidal variability of chlorophyll and SPM concentrations are comparable in magnitude. However, differences exist in the short-term dynamics of phytoplankton biomass and suspended sediment concentrations. Tidal advection is apparently the predominant mechanism of short-term phytoplankton variability (at least in the deep channel), whereas tidally-driven resuspension and riverine sources of sediments may be the important mechanisms of SPM variability. Finally, mechanisms of short-term seston variability may differ among bathymetric regimes, depending on water depth and the importance of benthic sources and sinks.

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